

Carbon sequestration in mangrove forests

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Daniel M Alongi*

Mangrove forests are highly productive, with carbon production rates equivalent to tropical humid forests. Mangroves allocate proportionally more carbon belowground, and have higher below- to above-ground carbon mass ratios than terrestrial trees. Most mangrove carbon is stored as large pools in soil and dead roots. Mangroves are among the most carbon-rich biomes, containing an average of 937 tC ha⁻¹, facilitating the accumulation of fine particles, and fostering rapid rates of sediment accretion (~5 mm year⁻¹) and carbon burial (174 gC m⁻² year⁻¹). Mangroves account for only approximately 1% (13.5 Gt year⁻¹) of carbon sequestration by the world's forests, but as coastal habitats they account for 14% of carbon sequestration by the global ocean. If mangrove carbon stocks are disturbed, resultant gas emissions may be very high. Irrespective of uncertainties and the unique nature of implementing REDD+ and Blue Carbon projects, mangroves are prime ecosystems for reforestation and restoration.

Mangrove forests are the only woody halophytes that live in salt water along the world's subtropical and tropical coastlines. Coincidentally, poverty and dense human populations flourish along these low-latitude coasts, partly explaining the high (1–3%) annual deforestation rates of these tidal forests. Mangroves are true ecotones, having some components of both marine and terrestrial biomes, but have also developed a number of unique structural and functional adaptations, such as viviparous embryos, physiological mechanisms to tolerate salt and aerial roots that enable the plants to respire in anoxic, waterlogged soils [1]. Mangroves are architecturally simple compared with terrestrial forests, usually harboring few tree species and lacking an understory of ferns and scrubs. However, the standing biomass of some mangrove forests in equatorial regions can be immense, rivaling the height and weight of many tropical rainforests [1].

Mangroves are ultimately limited by temperature but, at local and regional scales, variations in precipitation, tides, waves and river flow greatly determine their expanse and biomass. Attempts have often been made to classify the sequential changes in forest structure and species distribution parallel to shore but, in reality, most mangrove

forests represent a continuum of types in relation to gradients in their physical settings. Variations can be expressed within a single estuary, where there are usually upstream–downstream changes in geomorphology, salinity, waves, tides and river flow, with these factors affecting water circulation by generating mixing and trapping of **coastal** water [2]. The development of mangrove forests occurs where near-horizontal topography coincides with sea level; a relatively stable period of sea level is, thus, a prerequisite for the development of old-growth forests [3]. The response of mangroves to environmental change is, therefore, often indicative of past changes in coastal conditions, especially in sea level. Comparing present patterns in forest species with paleoecological information provides considerable insight, not only into how mangroves responded to past sea level changes, but how they may respond to climate change in the future.

Human disturbance obscures natural change and our ability to distinguish one from the another is limited, as most forests have a history of both natural and human disturbances, and are often intertwined and indistinguishable. Mangroves are naturally disturbed by tsunamis, floods, cyclones, lightning, pests and disease,

*Australian Institute of Marine Science, PMB 3, Townsville MC, Queensland 4810, Australia
E-mail: d.alongi@aims.gov.au

Key terms

Mangroves: Trees and associated plants, microbes and animals that live at the interface between land and sea. These tidal ecosystems have both semi-terrestrial and marine components.

Coastal: Land, water and aquatic habitats that reside where the continents meet the ocean. These habitats are usually only a few kilometers in width but are highly dynamic and interactive with respect to energy and material flow between land and sea.

Carbon sequestration: Term used to describe the acquisition and storage of carbon. Refers most often in relation to the ability of ecosystems to reduce the impact of increasing CO₂ concentrations in the atmosphere.

and become more susceptible when human stressors such as pollutants are introduced. However, mangroves often exhibit considerable resilience to disturbance, undergoing perpetual change in ecosystem development commensurate with the evolution of the environmental settings they inhabit, and are, thus, mosaics of successional stages arrested or interrupted over time and space by natural ecological responses in relation to disturbances both large and small [4].

Mangrove forests are a valuable ecological and economic resource, providing essential services such as food and fuel resources; nursery grounds for fish, mammals and

other semi-terrestrial and aquatic fauna; depocenters for sediment, carbon and other elements; and, in some instances, offering some protection from coastal erosion due to tsunamis and intense tropical storms [1]. Despite their uses to humans, approximately 50% of the world's mangrove forests have disappeared over the past 50 years [5], ironically reflecting their importance as a valuable economic resource. Major causes for this destruction have been urban development, aquaculture, mining, and overexploitation of timber, fish, crustaceans and shellfish. The average monetary value of mangroves has been estimated as second only to the value of estuaries and seagrass meadows, and greater than the economic value of coral reefs, continental shelves and the open sea [6].

Of greater eventual value is the role of mangroves in storing carbon to help ameliorate the impact of climate change. There is a growing consensus that it will be impossible to achieve significant cuts in GHG emissions without passive and active means to capture and store CO₂ [7]. The role of carbon storage in mangroves has often been overlooked and either underestimated or overestimated [1], and it is the purpose of this review to critically assess the role of mangroves in **carbon sequestration** and its global significance.

Carbon production

Mangroves are usually highly productive forests and, as a significant fraction of their soil carbon is plant-derived [8], it is crucial to assess rates of net primary productivity of mangroves and associated plants, especially benthic microalgae. Measurement of primary production in mangrove forests is limited by methodological shortcomings, but the best estimates suggest that mangrove carbon production is more rapid than other estuarine and marine primary producers [9]. Rates of mangrove net

primary production (NPP) based on different methods range from 0.5 to 112.1 t dry weight (DW) ha⁻¹ year⁻¹ but most methods either significantly overestimate (the light attenuation method) or underestimate (litterfall) the true rates of production.

The most reasonable means at present to assess NPP of forests is to measure aboveground biomass accumulation plus litterfall, and there are quite a number of such measurements for both mangroves and tropical terrestrial forests. For mangroves, the mean rate of aboveground NPP is 11.1 t DW ha⁻¹ year⁻¹ with a median value of 8.1 t DW ha⁻¹ year⁻¹; for tropical terrestrial forests, the mean rate of aboveground NPP is 11.9 t DW ha⁻¹ year⁻¹ with a median value of 11.4 t DW ha⁻¹ year⁻¹; for both mangroves and terrestrial forests, NPP declines with increasing latitude [1]. Considering the differences within and between both forest groups in biomass, height, age and species, the rates are very close and clearly imply that rates of NPP are equivalent between mangroves and other forests.

Like other forests, mangroves vary in size and age and, therefore, vary in rates of production and in the balance between carbon production and respiration. The few studies that have measured mangrove tree growth over time or in stands of known age have observed stand dynamics similar to other forests, identifying stages of early rapid growth during colonization and early establishment, followed by a slow decline in growth rate into maturity and senescence [1,10,11]. The stable-state maturity phase can be prolonged in some mangrove stands and may represent an alternate succession state in which the clock for the climax stage is reset by successive disturbances [10]. The relationship between mangrove forest age and photosynthetic production [11] suggests prolongation or arrested progression when forests are disturbed; *Rhizophora apiculata* forests in southeast Asia show log-phase photosynthetic rates until approximately 20 years, after which photosynthesis levels off but does not significantly decline for nearly a century [1]. These data imply that mangroves might indeed constitute a carbon sink for up to a century if left relatively undisturbed.

Other primary producers inhabit mangrove forests and their rates of NPP can be significant, especially in comparatively open canopies and on tidal banks where sufficient light penetrates to the forest floor [1]. Various autotrophic and mixotrophic microbes and microalgae, as well as macroalgae, live on the soil surface and as epiphytes on tree parts, especially aerial roots and decomposing wood. The quantitative contribution of these smaller autotrophs is dwarfed by tree production, but belies their importance as food and refugia for consumers. However, some evidence suggests that they can play an important role in soil carbon and nitrogen cycling, especially when found as intact mats [12].

Carbon allocation & ecosystem storage

Critical to our ability to estimate the role of mangroves in coastal and global carbon cycling is an accurate understanding of where carbon fixed by the trees is allocated. Like other woody plants, mangroves construct new foliage, reproductive organs, stem, branches and root tissues and maintain existing tissue, as well as creating storage reserves and providing chemical defense. Approximately half of all CO₂ assimilated by mangroves is returned to the atmosphere via above- and below-ground respiration [1,11]. This is only a crude estimate owing to the lack of empirical data and the difficulty of measuring root processes and respiration of woody parts. The proportional allocation of fixed carbon within trees varies with many factors, such as light intensity, species composition, nutrient and water availability, salinity, tides, waves, temperature and climate [11].

The greatest unknown with regard to carbon allocation is root production, which is difficult to measure, especially in waterlogged soils. The few studies that have measured root growth *in situ* estimated rates ranging from 18 to 1145 g DW m⁻² year⁻¹ with most estimates between 300 and 380 g DW m⁻² year⁻¹ [1]. These estimates are at the lower end of the range of values measured in tropical terrestrial forests [13]. However, most measurements were made in mangrove fringe stands, so it is likely that the growth and production of mangrove roots is similar to their terrestrial counterparts. A recent analysis of carbon allocation suggests that mangroves allocate proportionally more carbon belowground than terrestrial trees [14].

Carbon inventories from a number of mangrove ecosystems show that both above- and below-ground biomass increases, and that the ratio of below- to above-ground biomass decreases with increasing stand age (Table 1). These data show that belowground carbon biomass is, on average (mean = 1.3), equivalent to carbon allocated aboveground; other studies have indicated that more carbon biomass is allocated belowground [15–18] supporting the notion that mangroves store a disproportionate fraction of fixed carbon underground. Further, the amount of soil carbon increases with forest age (see Figure 5.1 in Alongi [1]).

Complete inventories of ecosystem components show that carbon fixed within the forest, as well as carbon imported from adjacent terrestrial and marine waters, are stored as large pools of soil carbon [19,20]. Analysis of carbon in *Rhizophora stylosa* and *Avicennia marina* in arid coastal areas of Western Australia [19] and in *R. apiculata* forests in southern Thailand [20] showed that although most carbon was unassociated with roots, the majority (75–95%) of tree carbon belowground was vested in dead, rather than live, roots. The Thai study also showed that the soil and dead root carbon pools increased in size with increasing stand age [20].

A recent assessment of carbon stored in various forest domains found that in comparison with boreal, temperate and tropical upland forests, mangroves throughout the Indo-Pacific are among the most carbon-rich forests in the tropics containing, on average, 1023 tC ha⁻¹, most of which is stored in soils >30 cm deep [21]. Adding published and unpublished data by authors from southern China, Vietnam, Indonesia, arid Western Australia, Queensland, Thailand and Malaysia (Table 1) to the data set of Donato *et al.* [21] to diversify the geographical, subtropical and arid-zone forest domains, we obtain a revised mean whole-ecosystem carbon storage estimate of 937 tC ha⁻¹ (Figure 1), which still indicates that mangroves are among the world's most carbon-rich forests. It is possible, of course, this statement may not hold true globally, especially when data is obtained from Central and South America and Africa, and from more forests in the arid tropics and subtropics where fringing mangroves and mangroves growing on hard and/or substrates of limited depth are common. Nevertheless, throughout the equatorial regions (e.g., the wet tropics of southeast Asia) it is true that mature mangrove stands attain highest carbon mass compared with other carbon-rich ecosystems, such as tropical rainforests.

What does inarguably appear to be a global pattern among mangrove forests is that their belowground pools of root and soil carbon are large, having a higher below- to above-ground carbon mass ratio than any other woody vegetation [22].

With the bulk of belowground carbon stored in dead roots and soil rather than in live roots, mangroves have a tendency to accumulate carbon relatively quickly. Belowground roots may only represent approximately 10–15% of total tree biomass, but the allocation of fixed carbon to replace sloughed root hairs and fine roots is considerably greater [23,24]. Moreover, carbon concentrations in dead roots are greater than in live roots, suggesting that dead roots store proportionally more carbon [19,20].

Vertical profiles of live versus dead root matter in a number of mangroves show that most living roots are shallow, within the upper 0–40 cm of soil [1]. Most fine roots are dead, probably the net result of rapid root turnover coupled with slow rates of root decomposition [23]. Rates of belowground decomposition of fine and coarse mangrove roots are indeed slow, with most rates ranging from 0.07 to 0.17% root mass lost per day; only roots of *A. marina* decompose more quickly at rates varying from 0.09 to 0.34% root mass lost per day [1]. Roots decompose at equivalent rates regardless of intertidal elevation, but coarse roots decompose less quickly than fine roots. These slow decay rates explain the formation of peat in many mangrove forests as inputs must exceed decay rates in order for peat to accumulate [23–25].

Table 1. Whole-ecosystem inventories of above- and below-ground carbon biomass and soil carbon for natural and replanted mangrove forests.

Location	Dominant species	Age (years)	Total (tC ha ⁻¹)	AGB (tC ha ⁻¹)	BGB and soil (tC ha ⁻¹)	Roots/AGB (tC ha ⁻¹)	Roots (tC ha ⁻¹)	Soil (tC ha ⁻¹)	Soil depth (cm)
Peninsular Malaysia	<i>Rhizophora apiculata</i>	80	2205	312	1893	NA	NA	NA	3800
	<i>R. apiculata</i>	18	1117	193	924	NA	NA	NA	4000
	<i>R. apiculata</i>	5	479	87	392	NA	NA	NA	2800
Southern Vietnam	<i>R. apiculata</i>	6	1179	54	1125	NA	NA	NA	3400
	<i>R. apiculata</i>	20	979	72	907	NA	NA	NA	2750
	<i>R. apiculata</i>	35	1904	153	1752	NA	NA	NA	3600
Southern China	<i>Kandelia candel</i>	NA	619	64	555	2.0	130	425	1850
	<i>K. candel</i>	NA	391	43	348	2.2	94	254	1900
	<i>K. candel</i>	NA	332	7	325	1.1	8	317	1175
Indonesia	<i>Avicennia marina</i>	NA	437	24	413	NA	NA	NA	80
	<i>Rhizophora stylosa</i>	NA	703	19	684	NA	NA	NA	62
	<i>Sonneratia caseolaris</i>	NA	654	28	626	NA	NA	NA	1450
Southern Thailand	<i>R. apiculata</i>	25	808	138	670	1.0	142	528	1900
	<i>R. apiculata</i>	5	579	20	559	2.9	57	502	800
	<i>Ceriops decandra</i>	3	600	29	571	4.4	127	444	1000
Western Australia	<i>R. stylosa</i>	NA	863	115	621	1.1	127	621	1500
	<i>A. marina</i>	NA	662	55	515	1.7	92	515	775
Queensland, Australia	<i>R. stylosa</i>	NA	2139	297	1842	1.1	312	1530	3500

AGB: Aboveground biomass; BGB: Belowground biomass; NA: Not available.
Data from [48,50–54,101].

Why do mangrove forests have such large amounts of carbon vested belowground compared with terrestrial forests? The presence of a large pool of dead roots can serve as a nutrient conserving mechanism, and even large dead roots may serve this purpose. For instance, old root channels have been found in mangroves in central Belize with a proliferation of living roots among the decaying roots, taking paths of least resistance and recovering nutrients released from decomposing roots [25]. A large pool of belowground live and dead root biomass mixed with rich soils may reflect their numerous physiological and morphological adaptations to life in a harsh, saline waterlogged environment. Salt negatively affects water use and under such conditions it may be advantageous for mangrove trees to invest more fixed carbon in growing very expensive root systems that turnover rapidly in order to maximize water gain. Large reservoirs beneath the forest floor may also help to stabilize the trees and the entire ecosystem from the continual push and pull of the tides, wave action, coastal winds and tropical storms. It makes evolutionary sense for mangroves to invest in a large belowground pool of carbon biomass as an effective counterbalance to litter and carbon dis-

solved in interstitial water that is lost via the tides. Whereas tropical humid forests recycle nutrients by rapid soil decomposition of litter in a relatively thin humus layer, mangroves reclaim elements by way of

very tight cycling between roots and microbes several meters deep into the soil, possibly to curtail losses and to minimize energetic costs.

Mechanisms facilitating sediment accumulation

Lying at the interface between land and sea, it is hardly surprising that mangroves accumulate sediment and associated particulate elements, such as inorganic and organic carbon. What is surprising is that their presence actively facilitates the accumulation of materials [26]. Carbon is accumulated in mangroves by direct inputs of mangrove carbon to the soil pool and by increasing rates of mass sediment accumulation. Carbon produced by mangroves does have other flow pathways, such as consumption by living organisms, especially microbes. Carbon consumed is remineralized and either emitted back to the atmosphere as CO₂ or exported by dissolved inorganic carbon. Dissolved and particulate organic carbon is also exported by tides where it can be either deposited or eaten or mineralized offshore.

The amount of carbon stored in mangrove soils varies widely, from <0.1% by soil dry weight to >40% with a grand median of 2.2% [8]. A highly variable proportion of this carbon is mangrove-derived as organic matter is brought in by the tides from adjacent seagrass meadows, coral reefs, macroalgae, rivers and from land-based sources, and other marine environments [8]. The fraction of mangrove-derived carbon in forest soils depends on a number of factors, including location of the forest

Key term

Flocculation: Physical, chemical and microbial processes by which particles are cemented together; the term 'floc' refers to the cemented tuft-like mass.

in relation to the open coast, distance to adjacent aquatic habitats, tidal amplitude, forest position in the tidal seascape and productivity of primary producers [27].

Unconsolidated sediments accumulate in relation to the movement of the turbidity maximum zone, where incoming bottom flow meets outward river flow. Tidal mixing and pumping within the moving zone facilitate particle **flocculation** and settlement. Flocculation of particles begins at salinities <1, and small flocs and free particles move downstream where they aggregate with local particles [28]. As flocs get larger, they move toward the river bed where they are entrained back upstream by baroclinic circulation and even further upstream at flood tide due to tidal pumping [28]. As these flocs move into the forest on flood tides, turbulence generated by flow around the trees helps to maintain flocs in suspension [2]. Settling occurs quickly, facilitated by the sticking of microbial mucus in the soil surface and by pelletization by invertebrate excreta. Large quantities of nonflocculated particles are re-exported from the forest on ebb tide, but most stick to mucus at the water surface.

Mangroves thus actively capture silt, clay and organic particles, and are not just passive importers of fine particles [2,28]; mangrove vegetation has a profound impact on sedimentation. Large trees with complex root systems, such as *Rhizophora* species, facilitate the deposition of particles to a much larger extent than trees that are smaller and of much simpler architecture, such as *Cerriops* species. Until slack water, turbulent wakes created by tree trunks, prop roots and pneumatophores maintain particles in suspension, but most flocs settle within 30 min just before slack high tide [28]. Despite the pull of the ebb tide, most flocs are retained within the forest as water motion and turbulence necessary for their resuspension is inhibited by the high vegetation density.

Rates of soil accretion & carbon sequestration

Mangroves accumulate carbon in tree biomass, but much of this carbon is eventually lost in the short- and medium-term by way of clear-cutting and human use, decomposition and export to adjacent ecosystems. Over the long term, carbon is stored primarily belowground as soil carbon and, eventually, under the right conditions, as peat. There are a number of methods to measure soil accretion [29], but some are either highly inaccurate (a mass balance approach where carbon inputs minus

carbon losses equal carbon either buried or unaccounted for) or reflect mostly modern rates of accumulation (measurement of short-term sediment accumulation using sediment traps or changes in depth of the soil profile). Analysis of radioactive elements produced by fallout (excess ^{210}Pb and ^{137}Cs) from atomic bomb testing in the atmosphere coupled with estimates of soil carbon concentrations provide longer term estimates of accumulation and a chronology of sedimentation of up to a century. Such methods also have their pitfalls, including reliance on expensive analytical equipment, difficulty in interpreting radiotracer profiles in bioturbated and disturbed soils and in soils where there are vertical changes in grain size, and problems with error induced by compaction of sediments as a result of the coring process [29].

The rate of soil accretion in mangrove forests averages 5 mm year^{-1} , with 94 measurements out of a total of 139 ranging from 0.1 to $10.0 \text{ mm year}^{-1}$ (Figure 2). The median value is 2.7 mm year^{-1} with a few measurements showing net erosion (minimum value = $-11.0 \text{ mm year}^{-1}$) or massive accretion ($46.3 \text{ mm year}^{-1}$) in highly-impacted estuaries, such as those in southern China [30].

Frequency of tidal inundation is the primary factor controlling the rate of accretion [31–33]. Less frequent inundation by tides means less input of sediment particles; forests located in the high intertidal area experience less soil accretion than forests closer to mean sea level, such as fringing stands at the sea–forest interface. In fact, mangrove carbon often accumulates on adjacent margins and intertidal mudflats [34]. Often overlooked, because empirical data are rare, are contributions to vertical accretion from the growth of belowground roots

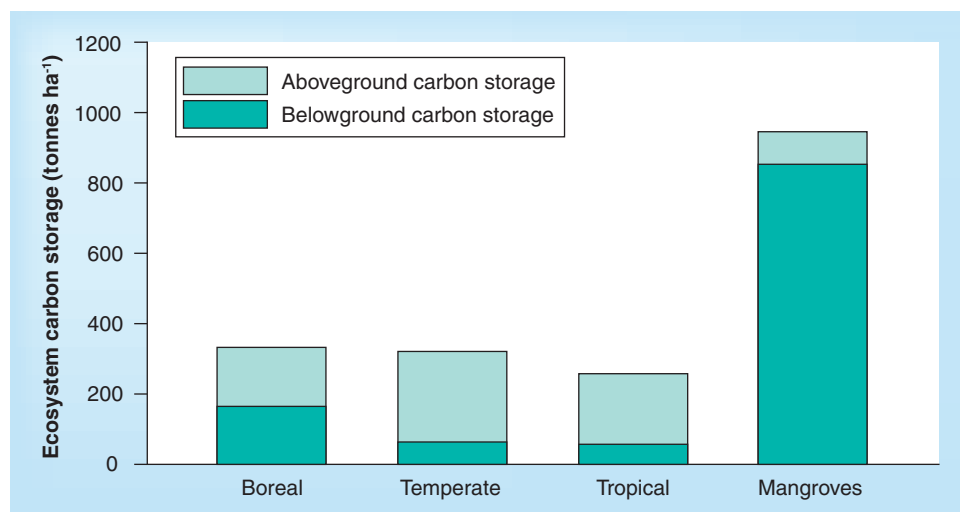


Figure 1. Differences in whole-ecosystem carbon stocks among boreal, temperate and tropical terrestrial forests, and subtropical and tropical mangrove forests.

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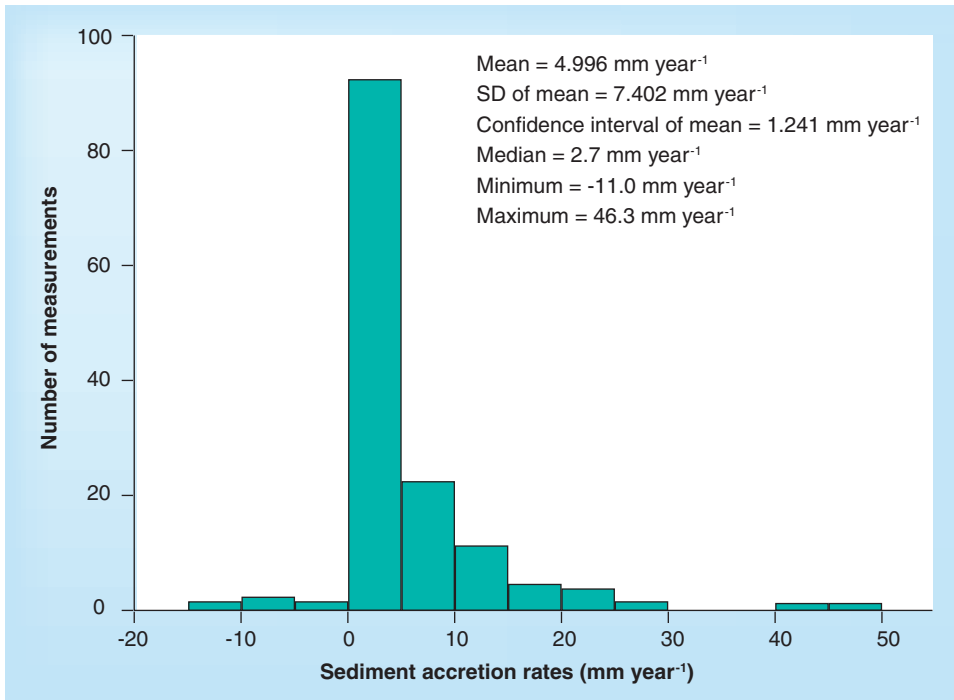


Figure 2. Sediment accretion rates measured in various mangrove forests worldwide (n = 139).

Data from [1,24,28–31,33,35,38,48,51,55].

and surface growth of microbial mats and turf algae and accumulation of litter. In some cases, such as in the Caribbean, contributions from these biological sources can be greater than accretion of mineral particles [33]. On other islands such those in the Federates States of Micronesia, natural subsidence plays a key role in overall rates of net elevation [35], although not the actual rates of soil accretion; nevertheless, such changes are important in determining the susceptibility of mangroves to changes in sea level [35]. Rates of soil accretion can vary over long timescales. In lagoon mangroves on the Yucatan Peninsula in Mexico, for instance, natural variations in accumulation rates and sources of soil carbon were detected over the past 160 years [36]. These changes corresponded to fluctuations in climatic variability in the region.

Mangrove sedimentation in relation to sea level rise was assessed by Alongi, who found that most mangrove forests were currently keeping pace with local rises in sea level [37]. However, there are a number of regions where sedimentation rates are lower than the rates of regional relative sea level rise, such as on some Pacific Islands [36] and at a number of mangrove stands in the Caribbean [33,38], although

accretion rates at a number of these endangered forests is higher than the eustatic sea level rise.

Available data on burial rates of carbon in mangrove ecosystems were first compiled by Twilley *et al.* [39], later updated by Jennerjahn and Ittekkot [40] and Duarte *et al.* [9], based on data in Chmura *et al.* [41]. Despite the different databases and methods used, all derived a similar estimate of a global carbon burial rate of approximately 23 TgC year⁻¹, which is equivalent to a rate of 167 gC m⁻² year⁻¹ assuming a total mangrove area of 137,760 km² [5]. Bouillon *et al.* [26,27] and Alongi [1] derived carbon burial rates of 18.4 TgC year⁻¹ (= 134 gC m⁻² year⁻¹) and 29 TgC year⁻¹ (= 211 gC m⁻² year⁻¹), respectively. Adding more recent data derived from radiochemical methods, we can revise the mean global burial rate for soil carbon to 24 TgC year⁻¹, equivalent to 174 gC m⁻² year⁻¹ with

values ranging from 10 to 920 gC m⁻² year⁻¹; the median burial rate was 16 TgC year⁻¹ (= 115 gC m⁻² year⁻¹). Like the sediment accretion data, the standard deviation exceeds the mean reflecting the high level of variability (and uncertainty) in carbon burial rates among forests worldwide. Nevertheless, most individual estimates (47 of a total of 66 measurements) are <200 gC m⁻² year⁻¹, with a minority of forests accumulating soil carbon faster (Figure 3), mostly in catchments heavily impacted by human activities, such as those in southern China [30] and in southeast Asia [42].

Significance of mangroves to terrestrial & marine carbon sequestration

How do these new estimates of carbon sequestration compare with other forested and coastal ecosystems? Globally, are mangroves a significant sink for carbon? Does their loss represent a significant return of CO₂ to the atmosphere?

The data presented here confirm the notion that mangroves are among the most carbon-rich ecosystems in the tropics. But at a global level, mangroves occupy only approximately 137,760 km², and a simple scaling up of the mean carbon burial rate equates to a global carbon sequestration rate of 13.53 Gt year⁻¹. The same exercise for boreal, temperate and tropical terrestrial forests extrapolates to global sequestration rates of 451.1, 327.6, and 422.4 Gt year⁻¹, respectively [43].

Key terms

REDD+: Acronym for Reducing Emissions from Deforestation and Forest Degradation. The + refers to the additional steps of conservation and the sustainable management of forests and enhancement of forest carbon stocks.

Blue carbon: Term coined to refer to steps designed to enhance the acquisition and storage of carbon in aquatic ecosystems, especially in coastal habitats such as seagrass beds and mangrove forests.

Thus, mangroves account for approximately 3% of carbon sequestered by the world's tropical forests, although they account for <1% of total area of tropical forests.

These data do, however, suggest the potential for significant GHG emissions if the high per-hectare carbon stocks of mangroves are disturbed. Losses of mangroves by clearing, conversion to industrial estates/aquaculture and changes in drainage patterns lead to dramatic changes in soil chemistry and usually result in rapid emission rates of GHGs, especially CO₂. For example, deforesting mangroves that grow on peat soils results in CO₂ emissions comparable to rates estimated from collapse of terrestrial peat soils [44]. Lovelock *et al.* measured CO₂ emissions from cleared mangrove peat soils in Belize on the order of 2900 tC km⁻² year⁻¹ [44]; this value compares well with CO₂ emissions measured from hurricane-damaged and aquaculture-impacted mangroves (1500–1750 tC km⁻² year⁻¹), rain-forests drained for agriculture (3200 tC km⁻² year⁻¹) and thawed Arctic tundra (150–430 tC km⁻² year⁻¹). Donato *et al.* [21] calculated a plausible range of CO₂ emissions of 112–392 tC released per hectare of mangrove forest and soils cleared, which gives a global emissions range of 0.02–0.12 PgC year⁻¹, assuming current deforestation rates (1–2% per year) and global area. This range is equivalent to at least 2–10% of global deforestation emissions (~1.2 PgC year⁻¹ [45]) and up to 50% of emissions from the world's tropical peatlands (0.24 PgC year⁻¹ [46]). These values are only indicative, as large uncertainties remain, including the accuracy of forest areas, temporal and spatial variations in fluxes and standing stocks, local and regional differences in the modes of disturbance, and variations in the depth to which soil is dredged.

If the contribution of mangroves to global forest carbon sequestration is very small, their contribution to carbon burial in the global coastal ocean is considerably greater. Compared with other coastal ecosystems, mangroves contribute an average of 14% to carbon sequestration in the world's oceans, although accounting for only 0.5% of total coastal ocean area (Table 2).

Even considering the large uncertainties in these estimates, the average burial rate of carbon in mangroves is

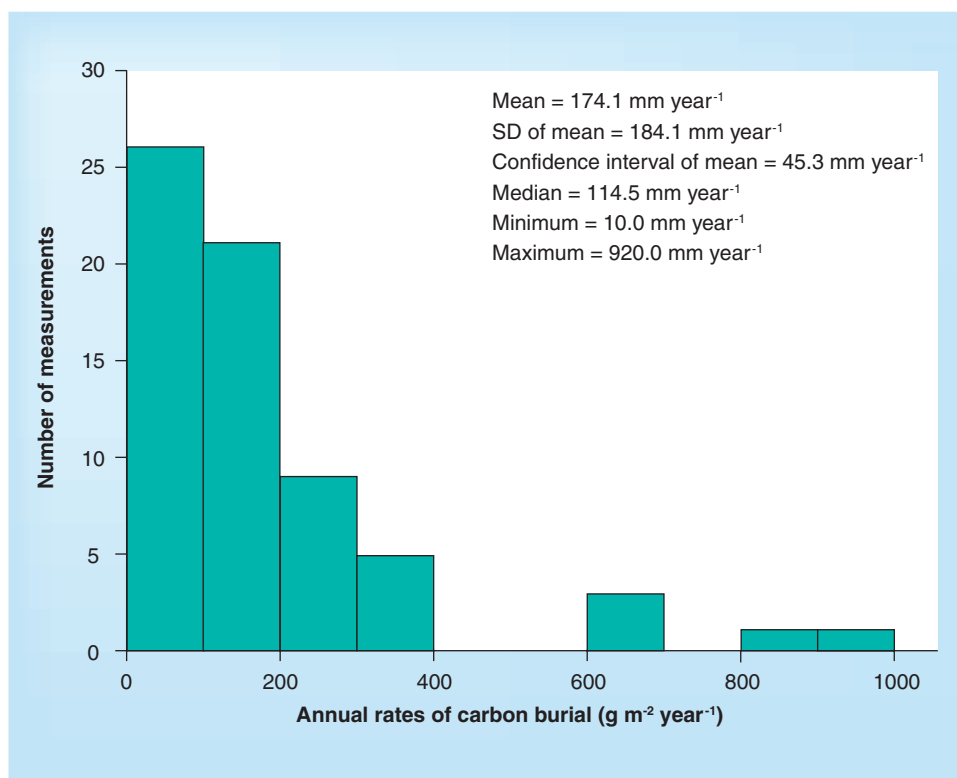


Figure 3. Annual rates of carbon burial estimated in various mangrove forests worldwide (n = 66).

Data from [1,9,15–18,21,25,28,30–32,34,38,41,42,48,51,55–59].

much greater than that from all other habitats, except for salt marshes. Therefore, considering the data in Figure 1 and in Table 2, mangrove forests have the highest area rates of carbon sequestration compared with any other ecosystem, terrestrial or marine, contributing disproportionately as a carbon sink.

Future perspective

Mangroves are currently being advanced as an essential component of climate change strategies such as REDD+ and blue carbon. McLeod *et al.* [47] and Alongi [48] have recently identified specific actions and issues that need to be addressed in blue carbon projects:

- Careful site selection, preferably at the seaward edge, based on drivers thought to affect carbon sequestration rates, such as frequency of tidal inundation, primary productivity and rates of exchange with adjacent ecosystems, as not all mangroves accumulate carbon;
- Measure and map the spatial and temporal variations in carbon stocks and burial rates, relating these factors to environmental and ecological drivers, possibly determining a set of indicators that can be used to quickly estimate changes in carbon stocks and fluxes;

Table 2. Global contribution of mangroves and other coastal habitats to carbon sequestration in the global coastal ocean.

Habitat	Area (10 ¹² m ²)	Sequestration rate (gC m ⁻² year ⁻¹)	Global carbon sequestration (Tg year ⁻¹)
Mangroves	0.14 (0.5%)	174	24 (14%)
Salt marshes	0.22 (0.8%)	150	33 (20%)
Seagrasses	0.3 (1.1%)	54	16 (10%)
Estuaries	1.1 (4.0%)	45	50 (30%)
Shelves	26 (93.6%)	17	44 (26%) [†]
Total			167

[†]Assumes that depositional areas cover 10% of total shelf area [9].
Data from [41,60–62].

- Remote sensing and aerial photography may be useful to facilitate changes in restoration/rehabilitation strategies, and in identifying changes in land use;
- Standardization of methods used to measure biomass and soil carbon stocks and rates of carbon burial;
- The execution of any scheme must consider modeled predictions of future climate changes, such as regional predicted rises in sea level;
- Planting of mixed species to maximize biodiversity, food web connectivity and net ecosystem production;
- Priority must be given to REDD+ schemes that give priority to old-growth forests as mangrove carbon stocks increase with stand age;
- Studies should be conducted concurrently to assess the conditions that determine whether or not climate change impacts such as changes in sea.

Future climate scenarios for the ocean are subject to large uncertainties, but regional changes in ocean circulation, temperature, salinity and pH patterns, and in sea level, must be considered as likely to have a strong impact on the ability of mangroves to sequester carbon [49]. Large uncertainties exist in our knowledge of carbon sequestration in mangroves, and such limitations must be factored into the blueprints of any payment for ecosystem services, blue carbon or REDD+ schemes. Only then will management of mangrove ecosystems be sustainable.

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The author has no relevant affiliations or financial involvement with any organization or entity with a financial interest in or financial conflict with the subject matter or materials discussed in the manuscript. This includes employment, consultancies, honoraria, stock ownership or options, expert testimony, grants or patents received or pending, or royalties. No writing assistance was utilized in the production of this manuscript.

Executive summary

Carbon production

- Mangrove net primary production averages 11.1 t dry weight ha⁻¹ year⁻¹, roughly equivalent to tropical terrestrial forests.
- Mangroves may constitute a carbon sink for up to a century.

Carbon allocation & storage

- Belowground biomass is equivalent to aboveground biomass in mangroves.
- Most carbon in mangroves is stored as large pools of soil carbon and belowground roots.
- Storage of carbon in mangroves averages 937 tC ha⁻¹.

Mechanisms facilitating sediment accretion

- Mangroves actively facilitate accumulation of carbon and other elements associated to fine particles.

Rates of soil accretion & carbon sequestration

- Rates of soil accretion in mangroves average 5 mm year⁻¹.
- Frequency of tidal inundation is the main factor controlling accretion.
- Global carbon burial rates for mangroves approximate 24 TgC year⁻¹.

Significance of mangroves to terrestrial & marine carbon sequestration

- Mangroves account for 3% of carbon sequestered by the world's tropical forests, but 14% of carbon sequestered in the world's ocean.
- If disturbed, mangroves may emit 0.02–0.12 PgC year⁻¹, equal to 2–10% of global deforestation emissions.

Future perspective

- Mangroves are prime candidates for REDD+ and blue carbon projects, but a number of issues and specific actions must be carefully addressed prior to commencement of such projects.

References

- 1 Alongi DM. *The Energetics of Mangrove Forests*. Springer, Amsterdam, The Netherlands (2009).
- 2 Mazda Y, Wolanski E. Hydrodynamics and modeling of water flow in mangrove areas. In: *Coastal Wetlands: An Integrated Ecosystem Approach*. Perillo GME, Wolanski E, Cahoon DR, Brinson MM (Eds). Elsevier, Amsterdam, The Netherlands, 231–262 (2009).
- 3 Ellison JC. Geomorphology and sedimentology of mangroves. In: *Coastal Wetlands: An Integrated Ecosystem Approach*. Perillo GME, Wolanski E, Cahoon DR, Brinson MM (Eds). Elsevier, Amsterdam, The Netherlands, 565–591 (2009).
- 4 Berger U, Adams M, Grimm V *et al.* Modelling secondary succession of subtropical mangroves: causes and consequences of growth reduction in pioneer species. *Persp. Plant Ecol. Evol. Syst.* 7, 243–252 (2006).
- 5 Giri C, Ochieng E, Tiszen LL *et al.* Status and distribution of mangrove forests of the world using earth observation satellite data. *Global Ecol. Biogeogr.* 20, 154–159 (2010).
- 6 Costanza RR, d'Arge R, deGroot R *et al.* The value of the world's ecosystem services and natural capital. *Ecol. Econ.* 25, 3–15 (1998).
- 7 Mills RM. *Capturing Carbon: The New Weapons in the War against Climate Change*. Columbia University Press, NY, USA, 465 (2011).
- 8 Kristensen E, Bouillon S, Dittmar T *et al.* Organic carbon dynamics in mangrove ecosystems: a review. *Aq. Bot.* 89, 201–219 (2008).
- 9 Duarte CM, Middelburg JJ, Caraco N. Major role of marine vegetation on the oceanic carbon cycle. *Biogeoscience* 2, 1–8 (2005).
- 10 Fromard F, Puig C, Mougin E *et al.* Structure, above-ground biomass and dynamics of mangrove ecosystems: new data from French Guiana. *Oecologia* 115, 39–53 (1998).
- 11 Clough BF, Ong JE, Gong WK. Estimating leaf area index and photosynthetic production in canopies of the mangrove *Rhizophora apiculata*. *Mar. Ecol. Prog. Ser.* 159, 285–292 (1997).
- 12 Joye SB, Lee RY. Benthic microbial mats: important sources of fixed nitrogen and carbon to the Twin Cays, Belize ecosystem. *Atoll Res. Bull.* 53, 1–24 (2004).
- 13 Perry DA, Oren R, Hart SC. *Forest Ecosystems (2nd Edition)*. Johns Hopkins University Press, Baltimore, MD, USA, 596 (2008).
- 14 Lovelock CE. Soil respiration and belowground carbon allocation in mangrove forests. *Ecosystems* 11, 342–354 (2008).
- 15 Fujimoto K, Imaya A, Tabuchi R *et al.* Belowground carbon storage of Micronesian mangrove forests. *Ecol. Res.* 14, 409–413 (1999).
- 16 Ren H, Chen H, Li Z *et al.* Biomass accumulation and carbon storage of four different aged *Sonneratia apetala* plantations in southern China. *Plant Soil* 327, 279–291 (2010).
- 17 Nguyen HT, Yoneda R, Ninomiya I *et al.* The effects of stand age and inundation on carbon accumulation in mangrove plantation soil in Namdinh, Northern Vietnam. *Tropics* 14, 21–37 (2004).
- 18 Ray R, Ganguly D, Chowdhury C *et al.* Carbon sequestration and annual increase of carbon stock in a mangrove forest. *Atmos. Environ.* 45, 5016–5024 (2011).
- 19 Alongi DM, Clough BF, Dixon P *et al.* Nutrient partitioning and storage in arid-zone forests of the mangroves *Rhizophora stylosa* and *Avicennia marina*. *Trees* 17, 51–60 (2003).
- 20 Alongi DM, Wattayakorn G, Tirendi F *et al.* Nutrient capital in different aged forests of the mangrove *Rhizophora apiculata*. *Bot. Mar.* 47, 116–124 (2004).
- 21 Donato DC, Kauffman JB, Murdiyarso D *et al.* Mangroves among the most carbon-rich forests in the tropics. *Nat. Geosci.* 4, 293–297 (2011).
- 22 Saenger P. *Mangrove Ecology, Silviculture and Conservation*. Kluwer, Dordrecht, The Netherlands, 342 (2002).
- 23 McKee KL, Faulkner PL. Restoration of biogeochemical function in mangrove forests. *Restor. Ecol.* 8, 247–259 (2000).
- 24 Cahoon DR, Hensel P, Rybczyz J *et al.* Mass tree mortality leads to mangrove peat collapse at Bay Islands, Honduras after Hurricane Mitch. *J. Ecol.* 91, 1093–1105 (2003).
- 25 McKee KL. Root proliferation in decaying roots and old root channels: a nutrient conservation mechanism in oligotrophic mangrove forests? *J. Ecol.* 89, 876–887 (2001).
- 26 Bouillon S, Rivera-Monroy VH, Twilley RR *et al.* Mangroves. In: *The Management of Natural Coastal Carbon Sinks*. Laffoley D, Grimsditch G (Eds). International Union for Conservation of Nature, Gland, Switzerland, 13–20 (2009).
- 27 Bouillon, S, Borges AV, Castaneda-Moya E *et al.* Mangrove production and carbon sinks: a revision of global budget estimates. *Global Biogeochem. Cycles* 22, GB2013 (2008).
- 28 Furukawa K, Wolanski E. Sedimentation in mangrove forests. *Mangroves Salt Marshes* 1, 3–10 (1996).
- 29 Bird MI, Fifield LK, Chua S *et al.* Calculating sediment compaction for radiocarbon dating of intertidal sediments. *Radiocarbon* 46, 421–435 (2004).
- 30 Alongi DM, Pfitzner J, Trott LA *et al.* Rapid sediment accumulation and microbial mineralization in forests of the mangrove *Kandelia candel* in the Jiulongjiang Estuary, China. *Estuar. Coast. Shelf Sci.* 63, 605–618 (2005).
- 31 Mahmood H, Misri K, Sidik BJ *et al.* Sediment accretion in a protected mangrove forest of Kuala Selangor, Malaysia. *Pakistan J. Biol. Sci.* 8, 149–151 (2005).
- 32 Ceron-Breton JG, Ceron-Breton RM, Rangel-Marron M *et al.* Determination of carbon sequestration rate in soil of a mangrove forest in Campeche, Mexico. *WSEAS Trans. Environ. Develop.* 7, 55–64 (2011).
- 33 McKee KL. Biophysical controls on accretion and elevation change in Caribbean mangrove ecosystems. *Estuar. Coast. Shelf Sci.* 91, 475–483 (2011).
- 34 Sanders CJ, Smoak JM, Naidu AS *et al.* Organic carbon burial in a mangrove forest, margin and intertidal mud flat. *Estuar. Coast. Shelf Sci.* 90, 168–172 (2010).
- 35 Krauss KW, Cahoon DR, Allen JA *et al.* Surface elevation change and susceptibility of different mangrove zones to sea-level rise on Pacific high islands of Micronesia. *Ecosystems* 13, 129–143 (2010).
- 36 Gonnea ME, Paytan A, Herrera-Silva JA. Tracing organic matter sources and carbon burial in mangrove sediments over the past 160 years. *Estuar. Coast. Shelf Sci.* 61, 211–227 (2004).
- 37 Alongi DM. Mangrove forests: resilience, protection from tsunamis, and responses to global climate change. *Estuar. Coast. Shelf Sci.* 76, 1–13 (2008).
- 38 Sanders CJ, Smoak JM, Naidu AS *et al.* Mangrove forest sedimentation and its reference to sea level rise, Cananea, Brazil. *Environ. Earth Sci.* 60, 1291–1301 (2010).
- 39 Twilley RR, Chen RH, Hargis T. Carbon sinks in mangroves and their implications to carbon budget of tropical coastal ecosystems. *Water Air Soil Pollut.* 64, 265–288 (1992).
- 40 Jennerjahn TC, Ittekkot V. Relevance of mangroves for the production and deposition of organic matter along tropical continental margins. *Naturwissenschaften* 89, 23–30 (2002).

- 41 Chmura GL, Anisfield SC, Cahoon DC *et al.* Global carbon sequestration in tidal, saline wetland soils. *Global Biogeochem. Cycles* 17, 1111 (2003).
- 42 Fujimoto K. Below-ground carbon sequestration of mangrove forests in the Asia–Pacific region. In: *Mangrove Management and Conservation: Present and Future*. Vannucci M (Ed.). United Nations University Press, Tokyo, Japan, 138–146 (2004).
- 43 IPCC. *Good Practice Guidance for Land Use, Land-Use Change, and Forestry*. Penman J, Gytarsky M, Hiraishi T *et al.* (Eds). IPCC, Kamiyamaguchi, Japan, 632 (2003).
- 44 Lovelock CE, Ruess RW, Feller IC. CO₂ efflux from cleared mangrove peat. *PLoS ONE* 6, e21279 (2011).
- 45 van der Werf GR, Morton DC, DeFries RS *et al.* CO₂ emissions from forest loss. *Nat. Geosci.* 2, 737–738 (2009).
- 46 Page SE, Rieley JO, Banks CJ. Global and regional importance of the tropical peatland carbon pool. *Global Change Biol.* 17, 798–818 (2011).
- 47 McLeod E, Chmura GL, Bouillon S *et al.* A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO₂. *Front. Ecol. Environ.* 9, 552–560 (2011).
- 48 Alongi DM. Carbon payments for mangrove conservation: ecosystem constraints and uncertainties of sequestration potential. *Environ. Sci. Policy* 14, 462–470 (2011).
- 49 Sen Gupta A, McNeil B. Variability and change in the ocean. In: *The Future of the World's Climate*. Henderson-Sellers A, McGuffie K (Eds). Elsevier, MA, USA, 141–165 (2012).
- 50 Alongi DM, Trott LA, Rachmansyah *et al.* Growth and development of mangrove forests overlying smothered coral reefs, Sulawesi and Sumatra, Indonesia. *Mar. Ecol. Prog. Ser.* 370, 97–109 (2008).
- 51 Alongi DM, Dixon P. Mangrove primary production and above- and below-ground biomass in Sawi Bay, southern Thailand. *Phuket Mar. Biol. Cent. Sp. Publ.* 22, 31–38 (2000).
- 52 Alongi DM, Sasekumar A, Chong VC *et al.* Sediment accumulation and organic material flux in a managed mangrove ecosystem: estimates of land–ocean–atmosphere exchange in peninsular Malaysia. *Mar. Geol.* 208, 383–402 (2004).
- 53 Alongi DM, Tirendi F, Trott LA *et al.* Benthic decomposition rates and pathways in plantations of the mangrove *Rhizophora apiculata* in the Mekong delta, Vietnam. *Mar. Ecol. Prog. Ser.* 194, 87–101 (2000).
- 54 Clough BF. Mangrove forest productivity and biomass accumulation in Hinchinbrook Channel, Australia. *Mangroves Salt Marshes* 2, 191–198 (1998).
- 55 Duarte CM, Kennedy H, Marba N *et al.* Assessing the capacity of seagrass meadows for carbon burial: current limitations and future strategies. *Ocean Coast. Manag.* doi:10.1016/j.ocecoaman.09.001 (2011) (In press).
- 56 Tateda Y, Nhan DD, Wattayakorn G *et al.* Preliminary evaluation of organic carbon sedimentation rates in Asian mangrove coastal ecosystems estimated by ²¹⁰Pb chronology. *Radioprotection* 40, S527–S532 (2005).
- 57 Xiaonan D, Xiaoke W, Lu F, Zhiyun O. Primary evaluation of carbon sequestration potential of wetlands in China. *Acta Ecol. Sinica* 28, 463–469 (2008).
- 58 Kauffman JB, Heider C, Cole TG *et al.* Ecosystem carbon stocks of Micronesian mangrove forests. *Wetlands* 31, 343–352 (2011).
- 59 Mitra A, Sengupta K, Banerjee K. Standing biomass and carbon storage of above-ground structures in dominant mangrove trees in the Sunderbans. *Forest Ecol. Manag.* 261, 1325–1335 (2011).
- 60 Matsui N. Estimated stocks of organic carbon in mangrove roots and sediments in Hinchinbrook Channel, Australia. *Mangroves Salt Marshes* 2, 199–204 (1998).
- 61 Kennedy H, Beggins J, Duarte CM *et al.* Seagrass sediments as a global carbon sink: isotopic constraints. *Global Biogeochem. Cycles* 24, GB4026, (2010).
- 62 Cai W-J. Estuarine and coastal ocean carbon paradox: CO₂ sinks or sites of terrestrial carbon incineration? *Annu. Rev. Mar. Sci.* 3, 123–145 (2011).

■ Websites

- 101 Data archives of the Australian Institute of Marine Science, 1979–1999. <http://data.aims.gov.au/metadataviewer/faces/search.xhtml>
- 102 Nature Geoscience. Supplementary data. www.nature.com/naturegeoscience